19 Decomposition models based on climatic variables, substrate variables, microbial respiration and production

P. W. FLANAGAN *University of Alaska, Fairbanks, Alaska 99701, U.S.A.*
F. L. BUNNELL *Faculty of Forestry, University of British Columbia, Vancouver, B.C., Canada*

Abstract

Results of our efforts to model decomposition in tundra are presented. Models were developed from field studies and specific laboratory analyses. Later, model predictions were evaluated against further field and laboratory data. Respirometric measures of decomposition and micro-organism metabolism are emphasized.

Introduction

The recognition that word models are an important initial step in the development of more rigorous mathematical models was explicit in the early stages of the International Biological Programme (Coloumbe & Brown 1970). The U.S. Tundra Biome's Decomposition Group and members of the International Tundra Working Groups on Decomposition and Microbiology initiated development of mathematical models in June 1972 (see Bunnell & Tait 1974 and Bunnell & Scoullar 1975 for a discussion of historical development). The objectives of these modelling efforts were essentially threefold:

(i) to explain seasonal and annual variations in decomposition rates;
(ii) to evaluate the influences on decomposition of moisture, temperature and substrate chemistry;
(iii) to incorporate explicitly microbiological data and relationships into a model which would facilitate intersite comparisons within tundra and allow extrapolation beyond the tundra ecosystem.

It was apparent that studies in weight loss were inadequate to address these three objectives.

Measures of weight loss integrate many simultaneously occurring phenomena and a large amount of variability within and between years is expected. The initial attempts at synthesis across a wide variety of tundra sites (Heal & French 1974) documented this tremendous variability. In developing the simulation models discussed here the approach was to relate specific processes to broad integrative measures within a biologically sound and mathematically rigorous framework. Thus, laboratory measures of specific processes, such as respiration and substrate utilization (Flanagan & Veum 1974; Flanagan & Scarborough 1974) could be related to field measures of weight loss (Bunnell & Scoullar 1975; Bunnell *et al.* in press and Bunnell *et al.* in press). Our premise was that the explicit recognition of component processes would account for the great variability in integrative measures (Bunnell & Tait 1974). In developing the models we have recognized two integrative approaches to decomposition studies. One holds that the total 'organic matter-microbial' complex respires measurable CO_2 in relation to climatic and state variables; the evolved CO_2 closely reflects the decomposition process and rate. The second approach states that the microbial biomass, annual productivity and associated respiration reflect the turnover rate of organic matter and when assessed in relation to annual primary productivity, inform us of the status of organic accumulation. Each broad approach can be stated as a complex hypothesis. Models incorporating either of these hypotheses can be tested for a variety of ecosystems. We have explored the hypotheses in relation to the tundra ecosystem particularly at Barrow, Alaska.

It is not the purpose of this paper to describe in detail the models built by the decomposition group of the U.S. IBP Tundra Biome Programme or the International Tundra Biome's Decomposition Working Group. The paper presents precis of two models, GRESP and DCOMP, which constitute a still evolving framework within which we are exploring decomposition processes and the possibility of developing an understanding of their role in ecosystems. The models were presented by Bunnell & Tait (1974), evaluated by Bunnell *et al.* (in press a and b) and examined within an ecosystem perspective by Bunnell & Scoullar (1975). The approach is strictly synecological and differs clearly from the approach of Marr *et al.* (1963). We also have employed data on growth kinetics of individual micro-organisms in the model of Marr *et al.* (1963) to simulate organism turnover rates in the tundra phyllosphere. This more autoecological approach has been used by several investigators in other ecosystems (Babiuk & Paul 1970; Gray & Williams 1971).

The general paradigms involved in most earlier models of decomposition (e.g. Jenny *et al.* 1949; Olson 1963; Minderman 1968; Jones & Gore, in press) were reviewed and compared to modelling within the Tundra Biome of IBP by Bunnell & Tait (1974). The models discussed in the present paper differ from earlier works in that the variations in decomposition rates are over short periods (daily) and explicitly acknowledge the influences of changing moisture, temperature and substrate quality. Further, they explicitly relate microbial processes such as respiration to broad patterns of weight loss. Bunnell & Tait (1974) discuss the merits of explicit versus implicit treatments of theory.

However, as have most earlier studies, the models GRESP and DCOMP ignore microfloral biomass. Other workers (e.g. Gray & Williams 1971) have brought attention to the difficulties encountered in relating field measures of annual microbial biomass transients and chemostat assessments of efficiency of microbial productivity and maintenance demands to field measures of primary productivity. Annual microbial maintenance demands calculated from chemostat determination of maintenance requirements may preclude growth of field microbial populations (Gray & Williams 1971). However, microbial growth is known to occur in the sites in question. Explanations offered for this paradoxical situation include: (i) underestimated productivity; (ii) conservative or inflated estimates of yield coefficient and maintenance demand respectively; (iii) no real accumulation of organic matter in the system, but a decrease; and (iv) inflated estimates of microbial biomass.

Here we test the model of Marr *et al.* (1963) using fungal measures from Barrow.

Laboratory, field and modelling methods

Microbial ecologists must brave a wavering episteme whenever laboratory studies of processes are related to field studies of the results of processes. Epistemological questions loom especially large when the relations are to be expressed unambiguously in mathematical models (Bunnell 1973). Gross as most field data are, they are 'real', integrated measures of decomposer activities and the influences of rate regulators upon them. We assumed respirometric measures of microbial activity to be especially 'real' and selected moisture, temperature and substrate quality as the most influential regulators of both respiration and weight loss. Using Gilson respirometers we examined influences of moisture, temperature and substrate quality on microbial respiration in above-ground substrates (Flanagan & Veum 1974; Bunnell *et al.* in press). These measures were incorporated in the models GRESP; DCOMP; as described by Bunnell *et al.* (in press, a and b).

Standing dead tissues were calculated in the manner described below. Before presenting the calculations for substrate availability it must be emphasized that the figures presented are subject to spatial and temporal variations within and between specific subsites of the Barrow intensive study site (Bunnell *et al.* 1975c). The study area referred to here is the same subsite of the Barrow intensive site referred to in Flanagan & Veum (1974) and Flanagan & Scarborough (1974). This subsite is an almost pure stand of *Eriophorum angustifolium* with randomly dispersed small (25–100 cm^2) patches of *Carex aquatilis*.

Approximately 100 $\mathrm{g\,m^{-2}}$ of new leaf tissue was produced annually on the site. The average standing crop of standing dead leaf tissue over four seasons was also about 100 $\mathrm{g\,m^{-2}}$ and on average was composed of 60, 32 and 11 $\mathrm{g\,m^{-2}}$ of leaves that were one, two and three years old respectively. Four-year-old standing dead leaves were rarely encountered. The between-year variation in amount of standing dead $\mathrm{m^{-2}}$ was relatively small (90 $\mathrm{g\,m^{-2}}$—118 $\mathrm{g\,m^{-2}}$).

In the absence of lemming influences, or production of new leaf materials, approximately 30% of the weight was removed as leachate from the standing dead zone by autumn (fall) rains and the freeze–thaw cycle leaving approximately 70 $\mathrm{g\,m^{-2}\,yr^{-1}}$ to become new standing dead tissue (all figures given are averages derived from four years of observation). Because standing dead vegetation did not accumulate from year to year we have assumed that on average the decomposition losses from standing dead approximate the rate of production, about 70 $\mathrm{g\,m^{-2}}$. Further, there is a loss of $70-60=10$ $\mathrm{g\,m^{-2}}$ of standing dead vegetation during the first growing season. The effects of intensive lemming grazing greatly alter the relationships outlined above (Bunnell *et al.* 1975c). However, during the period 1972 to 1974 inclusive lemming numbers were generally much lower than the pronounced cyclic highs noted by Pitelka (1973).

Annual and instantaneous moisture and temperature dependent weight losses in terms of CO_2 loss in respiration were determined earlier for standing dead leaves (Flanagan & Veum 1974; Bunnell *et al.* in press, a). In this study these values are compared with calculated respiration for fungal maintenance and production in standing dead leaf remains. The approach allows an evaluation of the model of Marr *et al.* (1963) for predicting organic turnover rates in a relatively simple natural system using empirical data concerning specific decomposer micro-organisms and their respiration in a native substrate.

Results and discussion

A. THE CHEMOSTAT MODEL

By examining growth, respiration, production efficiency and maintenance demands of individual micro-organisms in dead leaves and incorporating these data in a model we were able to predict annual weight losses in the leaf tissue. The model of Marr *et al.* (1963) states:

$$\frac{dx}{dt}+ax=y\frac{ds}{dt} \tag{19.1}$$

where $\frac{dx}{dt}$=instantaneous growth rate

a=maintenance demand ($g\,g^{-1}\,hr^{-1}$),
x=biomass of micro-organisms,
y=production efficiency or yield coefficient ($g\,g^{-1}$ substrate),
and $\frac{ds}{dt}$=instantaneous change in substrate.

If growth ceases then

$$\frac{dx}{dt}=0$$

and

$$\frac{ax}{y}=\frac{ds}{dt} \tag{19.2}$$

From growth and respiration measures of batch cultures (e.g. Fig. 19.1a and 19.1b) the values of 'a' and 'y' were calculated as $0{\cdot}32\times10^{-3}\,g\,g^{-1}\,hr^{-1}$ and $0{\cdot}35\,g\,g^{-1}$ substrate respectively. The average standing crop of fungi (x in equation (19.1) and (19.2)) determined by the Jones & Mollison (1948) technique was $0{\cdot}0045$ g fungal tissue per gram standing dead leaf tissue.

Using equation (19.2) we can calculate the rate of substrate utilization for maintenance of the microfungi per square metre of standing dead:

$$\frac{ds}{dt}=\frac{0{\cdot}32\times10^{-3}\,g\,g^{-1}\,hr^{-1}\times0{\cdot}0045\,g\,g^{-1}\times100\,g\,m^{-2}}{0{\cdot}35\,g\,g^{-1}}$$

$$=4{\cdot}1\times10^{-4}\,g\,hr^{-1}\,m^{-2}$$

Substrate utilization for maintenance over the active period of 120 days is thus $4{\cdot}1\times10^{-4}\,g\,hr^{-1}\,m^{-2}\times24\,hr\times120=1{\cdot}2\,g\,m^{-2}$, which leaves $70-1{\cdot}2$ or $68{\cdot}8\,g\,m^{-2}$ of substrate for growth.

To estimate the number of generations we can employ equation (19.3):

$$y(S+Nx)=Nx \tag{19.3}$$

where y and x are as equation (19.1),
S represents the amount of available substrate, and
N represents the number of generations.

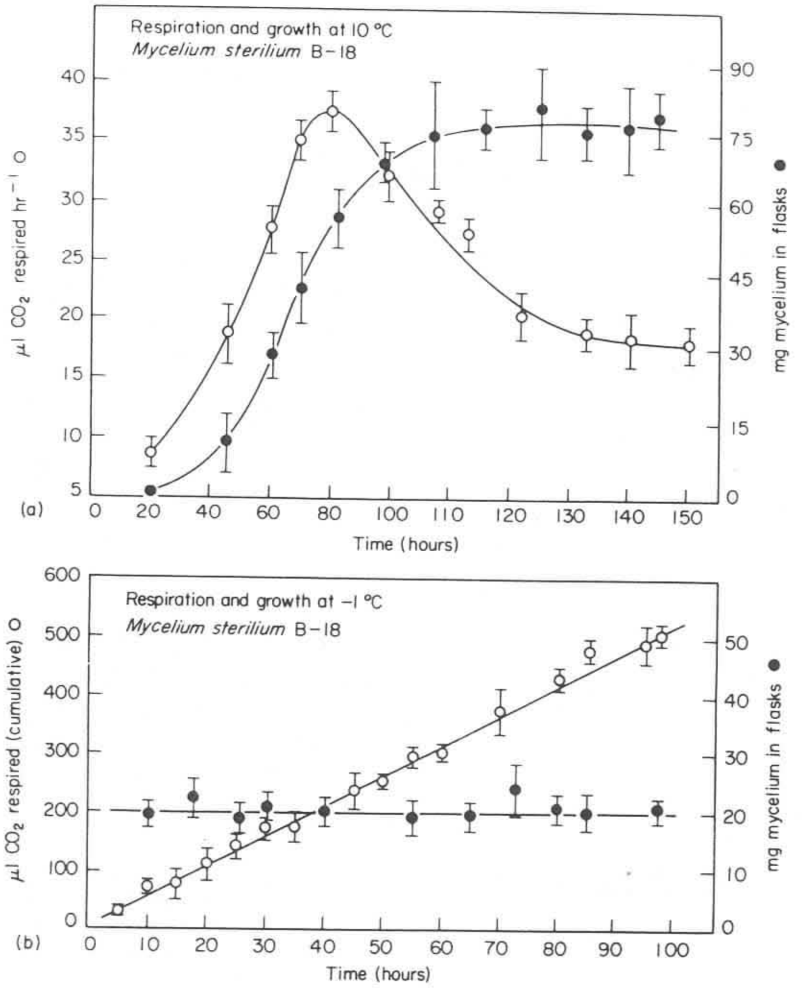


Figure 19.1. Respiration and growth of a common leaf litter fungus on Barrow tundra growing on a mineral salt medium containing a known glucose concentration. Vertical bars represent standard deviations.

Using a value of 68·8 for S, from equation (19.3), we obtain

$$N=\frac{ys}{X(1-y)}$$

$$=\frac{0{\cdot}35\,g\,g^{-1}\times 68{\cdot}8\,g\,m^{-2}}{0{\cdot}45\,g\,m^{-2}\,(1-0{\cdot}35\,g\,g^{-1})}$$

$$=82{\cdot}3 \text{ generations}$$

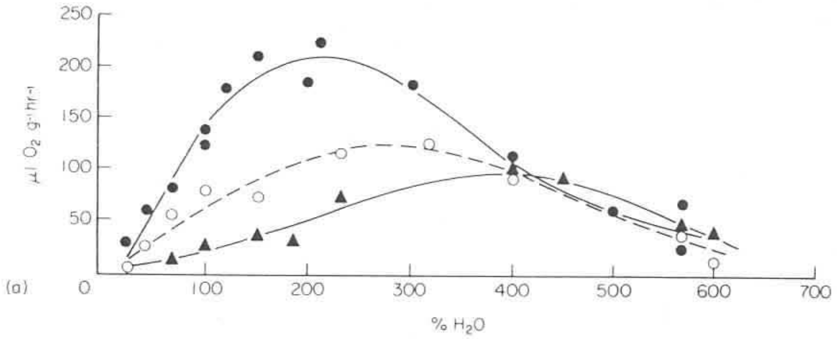
The computed number of generations corresponds to a renewal every 35 hours during the active season or a gross production of 37 g fungal tissue $m^{-2}\,yr^{-1}$.

However 37 g m^{-2} production of fungal tissue would result in 100% loss of standing dead leaves annually. The average annual loss in field leached standing dead is approximately 10 g m^{-2} as measured per unit length of marked dead leaves. Weight losses in litter below, measured in litter bags, is of the same magnitude. On this basis we have assumed that 8·8 g m^{-2} are available annually for microbial growth in standing dead tissue, allowing for 15 generations of the average standing crop m^{-2} of microbes or a production of 4·7 g m^{-2}. These predictions of microbial production are compatible with the availability of substrate and allow us to calculate a yield coefficient (*sensu* Heal & MacLean 1974) of $y' = 4{\cdot}7/8{\cdot}8 = 0{\cdot}54$. Unlike the yield coefficients of equation (19.1), and (19.2), y' allows the recycling of microbial tissue towards its own production. There appears to be no published estimates of fungal production in the vegetation canopy with which we can compare our results. It may be pertinent to note that our estimates of generation time do not fall within the range reported for Parinkina (1974) for bacteria in tundra soils.

To a limited extent we can evaluate the veracity and integrity of our assumptions by independent studies on microbial respiration in standing dead vegetation and weight losses from litter bags placed in the standing dead canopy. During the growing season of the first year following death, standing dead vegetation is diminished by about 10 g m^{-2} or about 14% (10 g m^{-2}/70 g m^{-2}). Flanagan & Veum (1974) predicted weight losses due to microbial respiration of 10·1 – 11·8% and reported measured weight losses from litter bags in the standing dead canopy of 9·9 ± 1·8%. These observations suggest that microbial respiration alone accounts for a significant proportion of the total weight lost, and do not contradict the assumptions made in equations (19.1), (19.2) and (19.3). The high proportion of weight loss due to microbial respiration is similarly compatible with the initial leaching losses (30%), largely complete by the beginning of the active growing season, and the relatively low abundance of invertebrate saprovores feeding aboveground (Bunnell *et al.* 1975c). In summary, we feel that careful examination of individual micro-organisms can lead to understanding of rates of decomposition and organic matter turnover at the 'macro' level of ecosystems. Admittedly the present study was relatively simple because of the single substrate and predominance of a few organisms (Flanagan & Scarborough 1974), but it does suggest that autoecological studies of micro-organisms can contribute to the understanding of rates often viewed at an ecosystem level.

B. MATHEMATICAL SIMULATION MODELS

Flanagan & Veum (1974) utilized empirical relationships to show that weight loss attributable to C loss in respiration was often close to weight losses measured in litter bags, particularly in material 1–3 years of age. They employed generalized moisture and temperature responses of tundra decom-



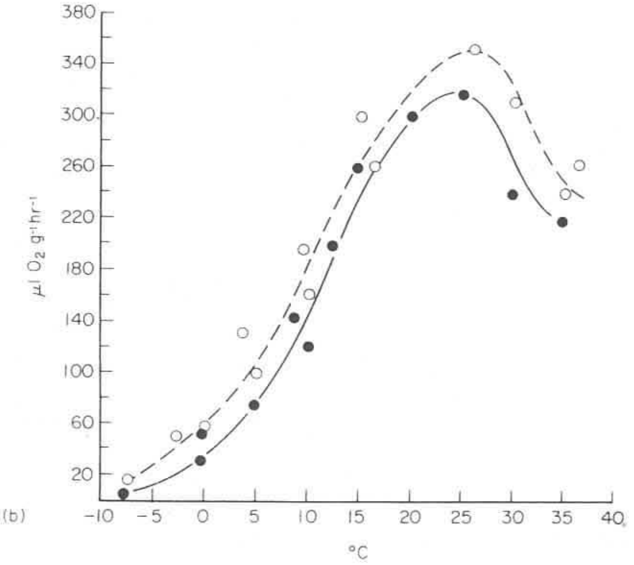


Figure 19.2A. Response of microbial respiration in Barrow litter at 0°C, (▲); 5°C, (○); and 10°C, (●), to changes in moisture content.

Figure 19.2B. Response of Barrow litters (⊙=*Carex aquatilis* and ●=total litter) at 120% H_2O (dry wt) to temperature variation. In A and B lines are plotted by hand and points represent the mean of ten samples each of which was read ten times during the experiments.

poser systems such as those illustrated in Fig. 19.2. Among the tundra mycoflora the Q_{10} value (averaged over 10°C increments from −10°C to 25°C) was 4. Respiration continued down to −5·0°C; was depressed by temperatures above 30°C and was greatest at 25°C. In general cardinal moisture levels were 20%, 200–500% and 1,000% respectively for minimal, optimal and maximal levels. Moisture and temperature responses were interdependent over a wide range of both parameters. Usually, increasing temperature shifted the optimal moisture range towards the Y axis as in Fig. 19.2a. From such data we constructed respiration response surfaces for litter and standing dead vegetation of varying substrate quality (e.g. Fig. 19.3).

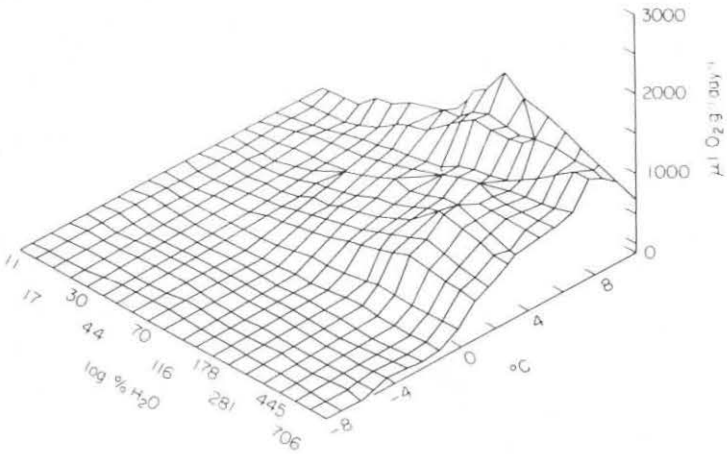


Figure 19.3. Response surface of microbial respiration versus temperature and moisture in total litter at Barrow. Each grid point represents an average of 6 to 30 replicates (Flanagan & Veum 1974).

Having documented general patterns and developed empirical models the next step was to relate specified processes within a biologically sound and mathematically vigorous framework (Bunnell & Tait 1974). The first model formulated was given the mnemonic GRESP because it was based largely on experimentation with Gilson respirometry. This model assumes that the major influences on microbial respiration are moisture, oxygen, temperature, and substrate. It incorporates the influences of these factors on microbial respiration as deduced from laboratory data and integrates the effects over climatic variation within a specific substrate and season to produce independent CO_2 based assessments of weight loss. These predicted losses generated from specific process studies can be related to the integrated weight loss as measured by litter bags.

(i) *The GRESP Model*

The rationale of the model is described in detail by Bunnell & Tait (1974) and Bunnell *et al.* (in press, a). High and low moisture levels adversely influence respiration rates. Equations (19.4) and (19.5) are first approximations of the moisture influence on microbial respiration as incorporated in the model. At moisture levels below optimum, respiration decreases according to equation (19.4), at high moisture levels respiration decreases according to equation (19.5). Thus, at low moisture levels the rate of moisture supply to respiring organisms is determined by coefficient a_1. Coefficient a_2 determines the supply of oxygen to micro-organisms under conditions of high moisture. Both coefficients in equations (19.4) and (19.5) are assumed to follow

Michaelis–Menten relationships with the percentage moisture content of the decomposing substrates.

$$WL = \frac{M}{a_1 + M} \tag{19.4}$$

where WL = water limitation reducing respiration,

M = % water content on a dry weight basis, and

a_1 = % water content at which the substrate is half 'saturated' with water.

$$O_a = \frac{M}{a_2 + M} \tag{19.5}$$

where O_a = oxygen availability,

M = % water content on a dry weight basis, and

a_2 = water content at which 50% of air spaces are water filled.

The proportion of free channels is therefore

$$1 - \left(\frac{M}{a_2 + M}\right) = \frac{a_2}{a_2 + M}$$

The substrate quality influences on respiration are expressed as

$$a_3 \times a_4^{T-10/10} \tag{19.6}$$

where a_3 = the optimal respiration rate at 10°C when neither H_2O nor O_2 are limiting,

a_4 = Q_{10} coefficient, and

T = temperature°C.

The formal statement of the respiration model is:

$$R(TM) = \frac{M}{a_1 + M} \times \frac{a_2}{a_2 + M} \times a_3 \times a_4^{T-10/10} \tag{19.7}$$

where $R(TM)$ = the respiration rate at temperature T and moisture level M.

Estimating model coefficients

Because of the model's nonlinear form, estimation of coefficient values (a_1 through a_4) requires nonlinear optimization techniques (Bunnell *et al.* in press a). Two determinants of the goodness of fit with respect to coefficients a_1 through a_4 were computed and designated r^2 and r_A^2. The coefficient of determination r^2 is not the square of the correlation coefficient used in linear regression but it can be used in the same way since it determines the proportion of variation in the data accounted for by the model. The statistic $r_A{}^2$ determines the proportion of 'accountable variation' in the data explained in the model. Its derivation is discussed by Bunnell *et al.* (in press, a).

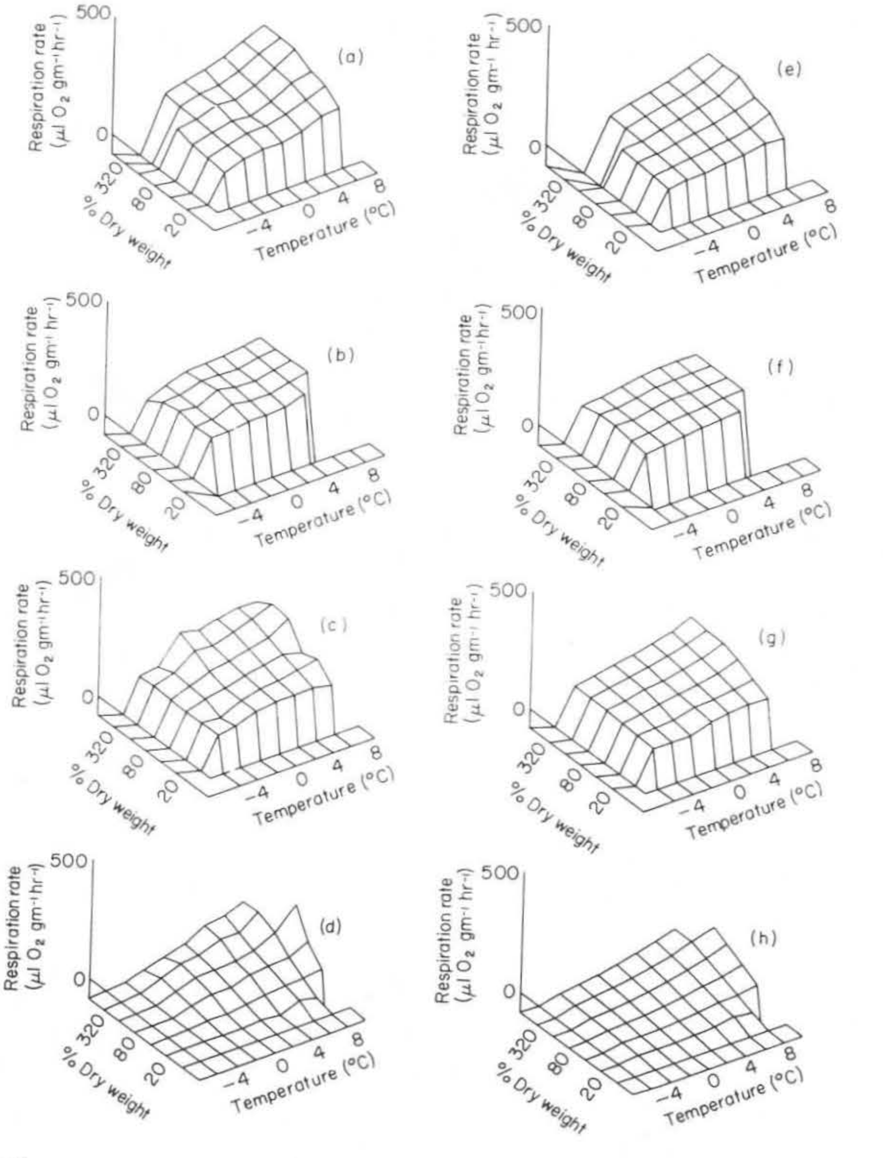


Figure 19.4. Measured (a–d) and simulated (e–h) rates of microbial respiration in standing dead of *Carex aquatilis* (a and e = 1 year old; b and f = 2 year old), and *Eriophorum angustifolium* (c and g) and total litter (d and h) at Barrow, Alaska (from Bunnell *et al.* in press, b).

Table 19.1. 'Goodness of Fit' of the GRESP Function to Data from Different Substrates. (Modified from Bunnell *et al.* in press, a.)

		'best' parameters					
Substrate type	Number of Observations	a_1 ($H_2O\%$ dw)	a_2 ($H_2O\%$ dw)	a_3 ($\mu l O_2\,g^{-1}\,hr^{-1}$)	a_4 (Q_{10})	r^2	r_a^2
Eriophorum (new)	54	416	416	777	8·79	0·65	0·96
Eriophorum (1 year old)	79	74	12,709	184	2·56	0·64	0·72
Eriophorum (2 years old)	65	19	3×10^9	107	2·79	0·72	0·77*
Carex (2 years old)	45	213	822	296	2·18	0·63	0·71
Dryas (2 years old)	38	160	160	158	1·75	0·36	0·43†
Carex (1 year old)	96	59	13,300	204	3·33	0·79	0·86
Total Barrow litter	346	116	2,820	232	3·74	0·66	0·71

* An optimum solution had not been found.

† The age of this material was in doubt and the number of treatment replicates at each observation point was only two.

In essence it approximates analysis of variance techniques in a nonlinear system, and permits sampling error to be removed from the fit between model and data. Measures of the goodness of fit of the model to data from different substrates are shown in Table 19.1. Examples of respiration response surfaces generated by the model are compared with measured surfaces in Fig. 19.4.

From Table 19.1, it can be seen: (i) that the model accounts for 71–96% of the accountable variation in respiration data; (ii) the model fits the respiration patterns of a number of diverse substrates equally well; (iii) that the coefficients a_1 through a_4 change between substrates and with age. In particular, it can be seen that as *Eriophorum* material ages, a_1 values decrease while a_2 values increase. As diminution and physical changes occur in the substrate the range over which moisture is not limiting to respiration increases. Bunnell & Tait (1974) predicted this phenomenon stating 'the more physically reduced and pitted the substrate the smaller will be the "field capacity" and the larger the "retentive capacity"'; (iv) a_3, a measure of substrate quality, decreases with age of *Eriophorum* substrate. There is a near linear relationship between the best fit value of a_3 and the percent ethanol soluble fraction as determined by Flanagan & Veum (1974) and (v) a_4 is usually higher for younger substrates (8·79 for freshly dead *Eriophorum*) than for older ones (2·56 for one-year-old *Eriophorum*).

Table 19.2. Results of sensitivity analyses on the GRESP model for total litter.

	Coefficient values that reduce the goodness of fit by 1% of the best value						Maximum departure from best value		
	Analysis number					best	Minimum	Maximum	Max–Min
Coefficient	1	2	3	4	5	fit	as % best	as % best	as % best
a_1 (H_2O% dw)	82	214	79	212	213	116	−32%	+84%	116%
a_2 (H_2O% dw)	4,293	1,085	5,192	1,101	651	2,820	−77%	+84%	161%
a_3 ($\mu l\ O_2/g/h$)	195	345	198	344	389	232	−16%	+68%	84%
a_4 (Q_{10})	3·8	3·6	3·8	3·8	4·1	3·7	−3%	+11%	14%

Sensitivity analyses employed in evaluating the GRESP model are described by Bunnell *et al.* (in press a). The results of sensitivity analysis (Table 19.2) indicate that microbial respiration in litter is much more sensitive to substrate and temperature variables than to moisture levels. Estimates of the sensitivity of the respiration rate to changes in the coefficients a_1 through a_4 decrease in the order a_4, a_3, a_1 and a_2, i.e. high moisture causing decreased O_2 availability has least influence on predicted respiration rates while temperature has the greatest influence.

These observations are companionable with the theoretical construction of the model and, together with the general goodness of fit of the model to data, indicate that the conceptual framework expressed by equation (19.7) is reasonably correct.

It is important to emphasize that the model is presently limited in several ways, particularly in its applicability to field sites where temperatures are often above 10°C. Further laboratory studies will increase its temperature range. The model does not consider anaerobic decomposition processes, does not account for influences of leaching and microfauna, and in general may underestimate total weight losses occurring during decomposition. The model's use is primarily one of estimating the proportion of weight loss attributable to loss of carbon via microbial respiration. For a specific substrate the closeness of this estimate to field measures of weight loss will reflect to some extent the magnitude of unaccounted microfaunal and leaching influences on decomposition. The model's prediction is substrate specific. Influences of variation in substrate quality on rates of decomposition are addressed by the first extension of GRESP, the model DCOMP.

It is a basic assumption of GRESP that the form of the respiration response is specific for a particular substrate. Acknowledging this assumption, the model may be employed to predict the respiration rate under any set of climatic circumstances. By employing the coefficients for Barrow total litter (Table 19.1), the temperature data for Barrow during 1971 (Weller *et al.* 1971) and moisture data of Flanagan & Veum (1974), a prediction of weight loss in total litter was made for the period 2 June through to 2 September 1971. The model predicted a weight loss of 13·4%. The prediction falls midway between independent measures in litter bag weight loss experiments of 9·9% ± 1·8% (Flanagan & Veum 1974) and 15% (Benoit *et al.* 1972). On the basis of this performance, it seems that the model can make realistic predictions for decomposition of a specific substrate during a season of known climatic conditions.

In this way interannual differences in weight loss can be related to climatic variation explicitly. Similarly the model allows examination of intraannual weight loss transients and inter- and intrasite variations. The influence of diurnal moisture and temperature patterns can be explored by the model. Bunnell & Tait (1974) have shown that there is a 12% increase in C loss from litter when computed using diurnal temperatures at two-hourly intervals as compared with average daily temperatures. Differences in diurnal climatic patterns may account for some between site variation in weight losses observed by Heal & French (1974). As expressed in equation (19.7) the model allows us to predict weight losses from a specific substrate (e.g. one-year-old litter or cellulose) placed in sites of different climate. Thus, we should be able to predict weight loss in Barrow litter placed, for example, in a tropical grassland. We could not predict weight losses in tropical grass litter unless we constructed respiration temperature/moisture surfaces for that litter.

Where substrate quality transients are steep during decomposition, due to fractions being removed by water flows, microfaunal activities, or to 'soft' substrate decomposition before recalcitrant substrate removal, then the GRESP model cannot be used to predict weight losses.

(ii) *The DCOMP Model*

A second model DCOMP has been designed to assess decomposition rates under the influence of changing substrate quality. The DCOMP model assumes that a decomposing substrate contains a number of basic chemical constituents each having a specific temperature–moisture–chemically determined respiration rate. Basically this concept is an extention of Minderman's (1968) hypothesis, first to include temperature and moisture influences and second, to relate a microbial process, respiration, to weight loss. We assume that the total respiration rate of a substrate containing several chemical groups will be the sum of the respiration of microbes using the different groups. Bunnell *et al.* (in press, b) have discussed several formulations relating substrate chemistry to microbial respiration and weight loss. The assumptions of the version discussed here are as follows: (i) each chemical category will have a temperature–moisture–respiration response surface of specific amplitude; (ii) each chemical response surface will have a similar shape and (iii) any two surfaces will differ in amplitude by a constant chemical-specific factor. The basic response surface used in DCOMP is the best fit of the GRESP model to Barrow total litter. It could just as well be the GRESP fit to cellulose placed in the field at Barrow. It should differ from a specific substrate's temperature–moisture–respiration response surface by a specific and computable constant.

The regression models used in calculating the respiration rate for specific chemical categories over varying temperature and moisture regimes are:

$$RR=\sum_{i=1}^{n} r_i x_i \qquad (19.8)$$

where RR = total respiration,

r_i = respiration rate of compound i, and

x_i = amount of compound i present.

To include the influence of temperature (T) and moisture (M) we write

$$RR(T,M)=\sum_{i=1}^{n} r_i(T,M)x_i \qquad (19.9)$$

To remove or account for the influence of T and M we write

$$\mathrm{RR}(\mathrm{T},\mathrm{M})=\sum_{i=1}^{n} b_i \mathrm{GRESP}(\mathrm{T},\mathrm{M})x_i \qquad (19.10)$$

In equation (19.10) the independent variables T and M are expressed as a surface such as those in Fig. 19.4, b=the ratio between the GRESP response surface for total litter and the response surface for compound i (i.e. a chemical specific scaler for the GRESP surface) and GRESP (T,M)= the underlying shape of the substrate specific response surface to T and M. For a substrate containing two different chemical groups, i.e. a 'soft' and a recalcitrant fraction we write:

$$\mathrm{RR}(\mathrm{T},\mathrm{M})=b_i \mathrm{GRESP}(\mathrm{T},\mathrm{M})x_i+b_j\ \mathrm{GRESP}(\mathrm{T},\mathrm{M})x_j \qquad (19.11)$$

where RR(T,M)=total predicted respiration in $\mu\mathrm{lCO_2\ hr^{-1}}$,
b_i=the ratio between the amplitude of the GRESP surface for total litter and the amplitude of the respiration response surface for the ethanol soluble compounds,
b_j=the ratio between the amplitude of the GRESP response surface for total litter and the amplitude of the respiration response surface for the recalcitrant compounds,
GRESP(T,M)=the response surface in $\mu\mathrm{lCO_2\ g^{-1}\ hr^{-1}}$ of respiration versus T&M for litter from Barrow (see equation (19.7)),
x_i=amount of ethanol soluble compounds i, and
x_j=amount of non-ethanol soluble compounds j

Regression analyses employing field data are summarized in Table 19.3. The regressions are of the form

$$\ln\ (\%\ \text{compound remaining})=b_0+b_1\ (\text{age in years}) \qquad (19.12)$$

The standing dead vegetation used in the analyses are *E. angustifolium* and *C. aquatilis*. Degrees of freedom are small because only one measure of chemical composition was associated with several measures of weight loss (Bunnell *et al.* in press, b). Nevertheless, slopes of all regressions depart significantly from zero ($\alpha = 0{\cdot}05$) which supports Minderman's (1968) hypothesis of exponential decay for specific chemical constituents. The different slopes or decay rates for cellulose placed in different portions of the system reveal the effects of different microclimatic regimes.

Results of analyses employing equation (19.10) are discussed in some detail by Bunnell *et al.* in press, b. Whereas equation (19.12) is simply a least squares fit to field measures, equation (19.10) posits a specific relationship between microbial respiration and abiotic variables, and sums the response of several component substrates. When the two broad chemical groups (equation (19.11)) were grouped by temperature and moisture classes significant relations ($\alpha=0{\cdot}05$) between respiration rate and chemical composition were observed in only one third of the classes.

These findings suggest that there is no simple underlying linear relationship between respiration rate and substrate composition. Broad relationships are, however, apparent. Regression analysis using equation (19.11) with 716 measured respiration rates and nine substrate types yielded coefficients of 3·8 and 0·76 for the ethanol soluble and non-ethanol soluble terms respectively. The associated t values were 5·9 and 15·2. With 7 d.f. we are confident that slopes of the regression differ from zero; $\alpha=0{\cdot}001$.

The model or equation (19.11) estimates the relative respiration rates to be 5:1 for ethanol soluble relative to the more recalcitrant fraction. This ratio approximates that observed for decomposition rates estimated from the standing dead data (0·69/0·12=5·75:1; see Table 19.3).

Table 19.3. Regression coefficients of ln (percent remaining) versus age in years. ln (percent remaining)$=b_0+b_1$ (age). (From Bunnell *et al.* in press, b.)

Substrate	Environment	b_0	b_1	r	Degrees of freedom	α
Cellulose	Standing dead	4·58	−0·015	−0·98	2	0·05
Cellulose	Litter layer	4·58	−0·036	−0·97	2	0·05
Cellulose	Soil	4·60*	−0·014	−0·997	1	0·05
Ethanol soluble	Litter layer	4·12	−0·69	−0·90	8	0·01
Non-ethanol soluble	Litter layer	4·56	−0·12	−0·68	8	0·05

* ln (100%)=4·605.

Assuming that both compound groups contain 45% carbon the respiration rates may be converted to weight losses by separately multiplying the two additive terms of equation (19.11) by

$$\frac{12\,\mu\text{gm C}}{22{\cdot}4\,\mu\text{l}\,CO_2}\times\frac{1\,\mu\text{g substrate}}{0{\cdot}45\,\mu\text{gC}}$$

and adding the two products.

Using field temperature and moisture data from Barrow the annual decomposition rates of the two fractions were computed to be 0·66 and 0·13 $g\,g^{-1}$ which is very close to the decomposition rates observed in the field (0·69 and 0·12 $g\,g^{-1}$; Table 19.3). Table 19.4 shows measured and simulated values for moisture–temperature–chemical specific rates of weight loss from *E. angustifolium* for the field season of 1973. Because it simulates respiration and thus decomposition rates for specific chemical components, the DCOMP model also predicts chemical composition (Table 19.4).

Table 19.4. Measured and simulated values for moisture–temperature–chemical specific rates of weight loss from *Eriophorum angustifolium*. Measured values use changes in identified age classes. Simulated values use abiotic data from 1973 to project loss rates (from Bunnell *et al.* in press, b).

	Measured %	Simulated %
% loss per year:		
ethanol soluble	49	48
non-ethanol soluble	11	12
Chemical composition of the substrate after one year:		
ethanol soluble	7	10
non-ethanol soluble	93	90
Total weight loss	27	31

The results summarized in Tables 19.3 and 19.4 document that there is reasonably close agreement between simulated weight losses and substrate composition and the measured values of these. Presently we can assume that the biological princip~~a~~les of decomposition are realistically formulated in the model structure. Also, it appears that chemical composition and, therefore, rate of decomposition loss for specific substrate components can be predicted providing temperature and moisture influences on microbial respiration are incorporated in the model. Consideration of the rates of decomposition losses for specific substrates need not be restricted to carbon compounds as we have done here. There are specific N and P requirements for the decomposition of ethanol soluble and the more recalcitrant substrates. Relationships between C losses and N and P losses formulated in a GRESP or DCOMP model would almost certainly lead to useful insights regarding mineral release from decomposing (respiring) tissues. Consideration of N and P losses accompanying respiration and the possibility of predicting N and P losses and content of substrates from respiration data form a rationale for continuing to develop GRESP and DCOMP as predictive tools for understanding the role and significance of decomposition in ecosystems.

Summary

GRESP and DCOMP have examined the climatic and substrate influences on decomposition rates and represent a more synecological approach than that of the chemostat model discussed earlier. Still, the range and rate of decomposition determinable or predictable using either method are very similar. By two dissimilar routes we have arrived at a similar assessment of decomposition rates for plant leaf tissue at Barrow, Alaska. The simulation models allow exploration of the role of major influencing factors on decomposition while providing a means of examining temporal and spatial variation in the rates of decomposition. Additionally these models allow us to predict overall rates of organic matter decomposition which if assessed in relation to productivity measures provide information on organic accumulation rates. The models ignore, amongst other variables, differences in microbial growth potentials. Rather, they sum all microbial growth potentials and incorporate the universal micro-organisms responding only to temperature, moisture and substrate variables. They thus represent a restatement of Winogradsky (1887) 'Everything is everywhere—the environment selects'.

Conversely, the model of Marr *et al.* (1963) examines microbial growth kinetics in relation to substrate availability ignoring the climatic and substrate quality influences on microbial growth potential. Whether we use one approach or the other we arrive at the same assessment of decomposition rates in the standing dead leaf remains. When we use both approaches we arrive at a paradoxical situation where we are unable to document what are the major determinants of decomposition rates—microbial population decomposition potentials or the influence upon these of environmental factors. It would appear that both constraints apply, particularly at the extremities of decomposition, but that the function decomposition proceeds virtually unregulated in rate across a wide spectrum of micro-organism and climatic variables, at least in tundra.

We may draw support for this statement by considering the breadth of the respiration versus moisture curve particularly at low temperatures (Fig. 19.2a). Also the influences of high and low temperatures are diminished by low and high moisture levels (Fig. 19.2a), and low and high moisture influences are counteracted respectively by high and low temperature levels (Flanagan & Veum 1974). To these observations we may add that micro-organisms in the tundra fall into three basic categories, i.e. psychrophiles, cold tolerant mesophiles and thermo tolerant psychrophiles (Flanagan *et al.* in prep.), and that individual micro-organisms contain different enzymes functioning optimally on specific substrates throughout a temperature range from −8°C to +35°C (Flanagan & Scarborough 1974). Acknowledging these observations it is clear that the range for micro-organism activity is indeed wide and that the influences of climatic and substrate variables upon it are masked because subtle enzymes activities grading to optima within and between micro-organisms occur throughout broad temperature and moisture ranges. The result of such activities and relationships produces a very broad 'optimal' mode for decomposition which lends itself well to prediction by relatively simple modelling techniques.

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